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OBSERVATIONS ON DIURNAL FOREST MOSQUITOES IN RELATION TO SYLVAN YELLOW FEVER IN PANAMA[1]

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INTRODUCTION

The recognition, in January 1949, of several human deaths of sylvan yellow fever in the Pacora area, some twenty miles east of Panama City, has served to focus attention on the lack of information in this region on the composition of the forest mosquito fauna and the nature of its activity. Such information is a fundamental preliminary to the understanding of the epidemiology of sylvan yellow fever in this area. There have been several studies of this sort conducted in South America, (Kumm and Novis, 1938; Bates, 1944; Laemmert, Ferreira and Taylor, 1946; Causey and Dos Santos, 1949), but the present one is in an area of critical interest, since the Isthmus of Panama, while still within the heart of the neotropical region, is the northwesternmost locality from which sylvan yellow fever has been recognized in the New World. The acknowledged South American vectors of sylvan yellow fever have been known in the literature on Panama only from scattered records, despite the activity over a period of half century of a series of excellent entomological collectors. This situation is understandable in the light of the fact that since the extirpation of urban yellow fever in Panama early in this century, the principal preoccupation of medical entomologists working in the area has been concerned with a better understanding of the mosquitoes involved in the transmission of another important mosquito-borne disease of the region, malaria. We have been more fortunate than our predecessors in the study of the mosquitoes of this area, in that during and since the period of the recent World War there has been a rapid expansion of roads and trails, giving us access to areas that previously could be reached with only the greatest difficulty. The reports of Clark, 1938, and Kumm and Crawford, 1943, called attention to the fact that sylvan yellow fever had been active in the region of Panama east of the Canal Zone in relatively recent times, but it has required the actual recognition of a group of human deaths to stimulate the support of a study of adequate scope to provide the background for the understanding of the epidemiology of the disease here.

The present authors contemplate a series of papers covering the entomological aspects of the problem, the first of which has already appeared (Galindo, Carpenter and Trapido, 1949). The present paper deals with the activities of the diurnal forest mosquitoes that relate to the possible vectorship by these insects of sylvan yellow fever in this area, and is based on a study that commenced in February

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1949 and was completed in February 1950. The distribution of the responsibility for the study among the authors was as follows. Galindo, through the Departamento de Salud Publica of Panama, provided one field crew of observers; Carpenter, through the U. S. Army, provided another; while Trapido, through the Gorgas Memorial Laboratory, provided a third. The nomenclatorial problems were worked out by Galindo, and the conclusions reached, represented by the names used, are his. The material from station K was examined by Carpenter, that from the stations H and J by Galindo, that from station F by Trapido, while Galindo and Trapido examined the material from the other stations. The compilation of the data and the preparation of the tables, text, and photographs were by Trapido. The planning of the study and the conclusions reached are shared in equal measure by the three authors.

METHODS AND PROCEDURE

A series of stations were established from sea level to 2100 feet in altitude in the area about twenty miles east of Panama City at and near the location where the group of fatal human cases of yellow fever had been recognized. In addition, a station was set up in the forest on the bank of the Chagres River near Juan Mina, Canal Zone, midway across the Isthmus, and yet another in the forest behind Fort Sherman, Canal Zone, on the Caribbean side of the Isthmus. These stations are located on Figure 1. Each station consisted of a tree in the forest to which was attached a platform about midway up the trunk and another in the crown of the tree, these being connected by stout ladders. These stations were designated by a letter followed by a number to indicate the altitude of the platform above the forest floor. Simultaneous catches were made of all mosquitoes either biting or approaching to bite human subjects used as baits, at ground level, and at the two tree platforms. Each station was operated one day each week throughout the one year period, from 8:00 A.M. to 5:30 P.M.

The general plan, with minor variations detailed below, was to have a crew of three men with a foreman-supervisor at each of these stations one day each week, from 8:00 A.M. to 5:30 P.M. The man at ground level, and those on each of the two elevated platforms, then caught all the mosquitoes which bit, or approached to bite, from the hour to thirty minutes after the hour, followed by a thirty minute rest period. Thus ten collections, each of half-hour duration, were made through the day at each level, at each station, each week, throughout the year-long period of the study. This routine was broken during periods of heavy rain that made collecting on the open platforms impossible, but in each case the foreman would make note of this fact, so that we might exclude these periods with no collections from our average of the catches. The collectors quickly learned to distinguish between the metallic colored species such as *Haemagogus*, *Aedes leucocelaenus* and certain of the sabethines, and the dun colored mosquitoes such as the species of *Taeniorhynchus*. The metallic colored species were collected individually in shell vials, 25 mm. x 80 mm., provided with a wad of moist absorbent cotton and a circle of filter paper in the bottom,

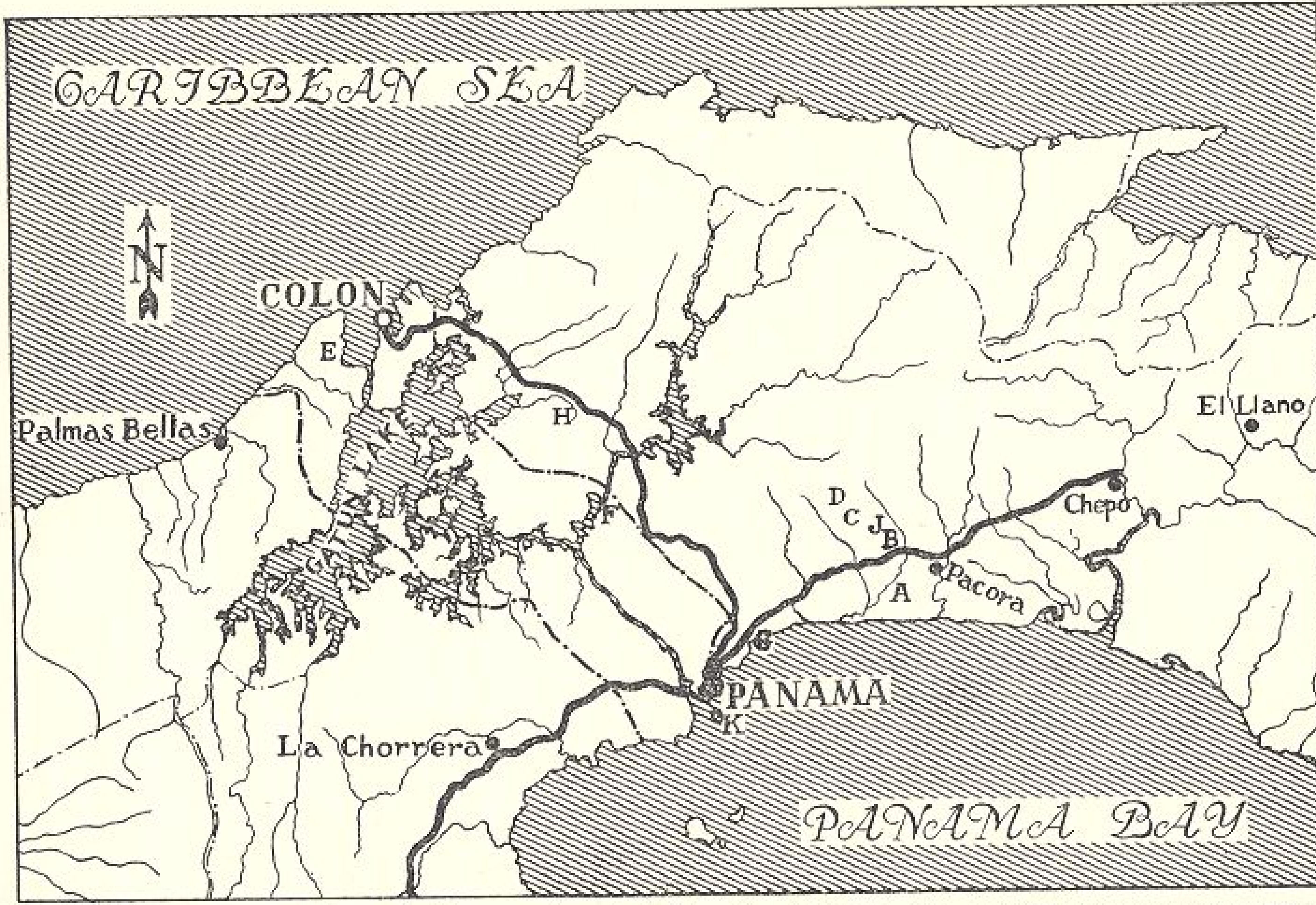

FIG. 1. The Panama Canal Zone and adjacent portions of the Republic of Panama. The location of the mosquito catching stations are indicated by letters.

and a stopper of wire-screen or a cotton plug. A small wad of absorbent cotton, moistened in sugar water, was then put on the top of the wire-screen, or the cotton plug was similarly moistened, so that the mosquitoes might feed. The collectors were provided with a stock of mimeographed forms on which they recorded the date and hour, the station and platform number, and their name. One of these slips was then attached to each vial with a rubber band and these accumulations of vials with living mosquitoes were brought into the central laboratory at the end of each day. The other mosquitoes were either collected with an aspirator tube and chloroformed, or killed directly by being collected with a chloroform tube. These were then transferred to pill boxes at the end of each half hour period, and the data on the date and hour, the station and platform number, and the name of the collector written on the cover of the pill box. The accumulated group of vials of living mosquitoes and the pill boxes of dead mosquitoes were brought into the laboratory at the end of each day, where they were examined, species identification made and recorded. It was necessary to collect the metallic colored species alive since at the start of the study we were uncertain as to which species of *Haemagogus* occurred in the study areas and we had no ready means of specific identification of these female mosquitoes. As all the members of our field crews had been vaccinated against yellow fever, we could then safely have them attempt to feed the mosquitoes by holding the vial containing the specimens against their arms or legs, since we wished to obtain eggs and subsequent progeny from these mosquitoes. At first the progeny of these mosquitoes were reared so that we might get larvae and adult males to make certain identifications. Subsequently we were able to work out adequate characters which enabled us to identify the adult females in the study areas and specific determinations were made directly on the specimens captured in the field.

The location and mode of operation of each of the stations follow.

Station A: This was located in the Pacora area near an abandoned airfield known as La Jolla No. 2. It was a few feet above sea-level and was operated on Monday of each week. The station here was an "espave" tree, *Anacardium excelsum* (Bert. & Balb.) Skeels., with one platform half way up the trunk, 20 feet above the ground, and a second platform 40 feet high, just under the forest canopy.

Station B: The series of stations lettered from "B" to "D" was located along a woods road, recently built, which gives access to a ridge now called Cerro La Victoria, between the Rio Juan Diaz to the west and the Rio Cabra to the east, while to north it is limited by the drainage of the Rio Cascades, a tributary of the upper Rio Chagres. These three stations are all on the side of the ridge draining to the Rio Cabra. The general region is twenty to twenty-five miles, and about fifty degrees east of north, from Panama City. Before the advent of the road, which has given us ready access to the area so that we might make collections on a routine weekly basis, this region was loosely spoken of as "Cerro Azul" and appears with that designation in various botanical and zoological publications. The natives of the region now commonly reserve the term "Cerro

Azul" for the ridges to the east of the Rio Cabra, while Cerro La Victoria rises to the west of this river. (Figures 2 and 3.)

The building of the road up the west side of this stream valley has given the local people access to the area, and has resulted in the clearing of the forest along the lower part of the course of the Rio Cabra, and the planting of the slopes beside the river in corn, upland rice, and some few patches of bananas. The "slash and burn" type of agriculture practiced here has moved up the valley each year and the land is either now planted, or reverting to second growth dominated by Cecropia trees, up to about 500 feet above sea-level. One of the fatal cases of yellow fever which occurred in November 1948 was a native working one of these clearings along the Rio Cabra at an altitude of 400 feet above sea-level. Subsequently, in March 1949, Dr. Herbert C. Clark, in the course of a survey of the animal reservoir of sylvan yellow fever (Clark, 1950), collected a number of monkeys and marmosets (white-faced monkeys, *Cebus capucinus capucinus* Linnaeus, Howling Monkeys, *Alouatta palliata aequatorialis* Festa, and Geoffroy's marmoset, *Marikina geoffroyi* Pucheran), a number of which gave positive neutralization tests for yellow fever, from within a quarter mile of this locality. We established our station B here at a tree a short distance from the stream, where a tongue of the forest projects down into the cleared fields. This station had one platform built 23 feet above the ground and a second near the top of the tree at 46 feet. This was operated on Tuesday of each week.

Station C: Above station B the slopes of Cerro La Victoria are covered with continuous virgin forest unbroken by clearing for agriculture and only disturbed by the access road with occasional lateral tractor trails to scattered cuttings of timber trees such as mahogany (*Swietenia macrophylla* King) and maria (*Calophyllum longifolium* Willd.), and small clearings which have been cut and leveled to provide sites for homes as part of a real estate development of the mountain. Station C was located in this tall forest at an altitude of 1200 feet above sea-level with a middle platform at 44 feet above the ground and an upper platform in a crotch in the crown of the tree at 71 feet (see Figures 4 and 5). This station was operated on Wednesday of each week.

Station D: The summit of the ridge at Cerro La Victoria is 2300 feet above sea-level and is exposed to far more wind than the slopes of the mountain. The more exposed places along the summit have a cover of low trees not exceeding 30 feet in height. Station D was located at 2100 feet and about 200 feet below the summit, in a ravine with taller trees somewhat protected from the wind, with one platform 26 feet and the other at 48 feet above the ground. Mosquito captures were made at this station on Thursday of each week. (Figures 7 and 8.)

Station E: This station was located on the Atlantic side of the Isthmus in the forest at the foot of a hill close behind Fort Sherman. It is only a few feet above sea-level. This is an area with almost twice as much rainfall as that experienced at the low altitude stations on the Pacific side. This station was operated only during the period from 10:00 A.M. to 12:30 P.M. because of the time consumed by the crew in traveling to the station from our base of operations on the Pacific side. The platforms here were at 28 feet and 46 feet above the ground. This

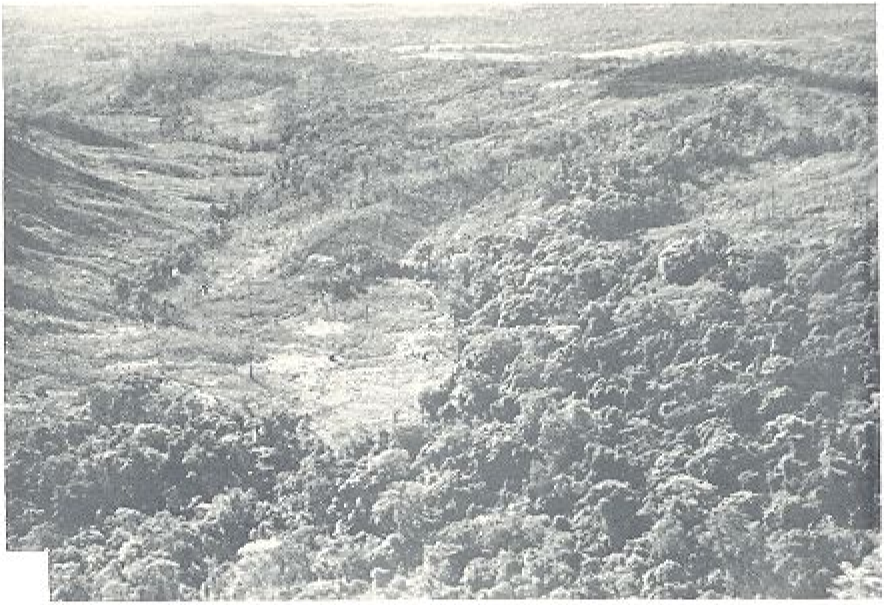

FIG. 2. (*upper*) Aerial view from above the forested slopes of Cerro La Victoria down the valley of the Rio Cabra. The extension of the "slash and burn" type of agriculture up the valley is shown. The elevation in the middle foreground is 400 feet. The Pacific side coastal plain may be seen in the far distance.

FIG. 3. (*lower*) Aerial view of the vicinity of station B in the valley of the Rio Cabra. The river marks the line between the fields in the foreground and the forest behind. The lower arrow points to the *bohio* of a native family working the fields. It was here that a fatal case of yellow fever occurred in November 1948. The upper arrow indicates the location of station B in the forest. In this forest 60% of the monkeys collected by Dr. Herbert C. Clark gave an immune reaction for yellow fever.

FIG. 4. Ladder and middle platform at station C, Cerro la Victoria, elevation 1200 feet. The middle platform here is 44 feet above the ground.

station was operated primarily to give a comparison of the forest mosquito population of the Atlantic side with that of the Pacific side and the Chagres River basin. Near the end of our study, however, in January 1950, a fatal case of

FIG. 5. The forest in the vicinity of station C at Cerro La Victoria is composed of large trees forming a covering canopy 80 to over 100 feet high.

yellow fever was recognized in a native from Palmas Bellas, on the Atlantic coast about nine miles from the location of this station.

Station F: This was established in the forest on the east bank of the middle

FIG. 6. Station F on the middle Rio Chagres near Juan Mina, Canal Zone. The middle and the upper platforms, F-26 and F-45, with the natives used both as bait and collectors, are shown.

Chagres River about a half-mile south of the Juan Mina Field Station of the Gorgas Memorial Laboratory. The platforms here were built on an "espave" tree at 26 feet and 45 feet above the ground, and the station was operated on

Friday of each week. This is in an area with rainfall intermediate between that at the Atlantic and the Pacific side stations. The elevation here is 100 feet above sea-level. (Figure 6.)

Station G: This was located in a mangrove swamp near the ruins of Panama Viejo five miles northeast from the present Panama City. No platforms were built at this station, but collections were made during the late morning and the middle of the day on Friday of each week. This station was established for the particular purpose of studying the biting habits of the mosquito *Haemagogus chalcospilans* Dyar which abounds in the mangrove swamps on the Pacific side of the Isthmus. This locality is at sea-level.

Station H: While the present study was in progress two fatal cases of yellow fever occurred during August 1949 in natives working in the forest between the Trans-Isthmian Highway and Gatun Lake near a settlement known as Buena Vista. In connection with an attempt to recover virus from mosquitoes in this area, platforms were built in four trees and collections made continuously every week-day from 8:00 A.M. to 4:00 P.M. These four trees are collectively designated at station H. The individual tree designations with the height of the platforms at which the collections were made, and the inclusive dates of their operation are as follows:

H-1, 66 feet, 19 October 1949 to 3 January 1950
H-2, 50 feet, 19 October 1949 to 3 January 1950
H-3, 64 feet, 19 October 1949 to 3 January 1950
H-4, 91 feet, 19 October 1949 to 14 November 1950

This locality is about 200 feet above sea-level. The data from these collections are presented to give a fuller picture of the arboreal mosquito population in the immediate area, and directly following sylvan yellow fever fatalities.

Station J: Six other trees were also selected on the forested slope of Cerro La Victoria about midway between stations B and C, and near station C and platforms built in them, in further efforts to collect large numbers of mosquitoes from the forest canopy for the attempted recovery of virus. These tree platforms are collectively designated as station J. The pertinent data on these tree platforms are as follows:

J-1, 49 feet, 19 October 1949 to 3 January 1950
J-2, 48 feet, 19 October 1949 to 3 January 1950
J-3, 48 feet, 19 October 1949 to 3 January 1950
J-4, 56 feet, 19 October 1949 to 3 January 1950
J-5, 54 feet, 1 December 1949 to 3 January 1950
J-6, 58 feet, 1 December 1949 to 3 January 1950

These trees were located in an area about 800–1200 feet above sea-level. Collections were made daily.

Station K: This was located on Flamenco Island, one of the three islands at the Pacific entrance to the Panama Canal, which is connected to the mainland by a causeway about two miles long. Collections of mosquitoes attacking man on the ground were made here on each week day from 9:00 A.M. to 3:00 P.M. This station was operated each week-day from December 2, 1949 to January 12, 1950 to give information on the biting habits of *Haemagogus argyromeris*.

FIG. 7. (*upper*) Aerial view of the crest of the ridge at Cerro La Victoria, elevation 2300 feet. The arrow indicates the location of station D below the summit in a protected ravine.

FIG. 8. (*lower*) Characteristic low scrubby forest along the summit of Cerro La Victoria. This may be contrasted with the much taller forest cover on the slopes of the mountain shown in Fig. 5.

CLIMATE OF THE STUDY AREA

The meteorological data presented in Table I are from the records of the Section of Meteorology and Hydrography of the Panama Canal and serve to give a general picture of the climate of the region during the year of the study.

Data presented are for the calendar year 1949 while the study covered the period from February 1949 to February 1950.

The Balboa Heights station is near the Pacific entrance to the Canal; the El Jefe station is at an altitude of 3200 feet on a ridge about five miles from our tree stations B, C, and D; the Madden Dam station is on the Chagres River near the middle of the Isthmus and about four miles from station F; the Cristobal station is at the Caribbean entrance to the Canal about two miles from station E. Reference to the total precipitation figures for the year will show the very large local variations in rainfall experienced in this restricted area. In general, the rainfall of the Caribbean side of the Isthmus is roughly twice that experienced near sea-level on the Pacific side, with the Madden Dam station, midway across the Isthmus, being intermediate. But the El Jefe station, the nearest to our principal study area at Cerro La Victoria, has a higher rainfall than that of the Caribbean side at sea-level. Only the El Jefe station, with 162.69 inches, had rainfall approaching that reported by Bates, 1945, from Villavicencio, Colombia, with a three year mean of 182.87 inches, where he conducted a similar study. The El Jefe station is on an exposed ridge at an altitude of 3200′ and undoubtedly experienced more rainfall than that which fell at the lower altitudes and more protected situations where our stations are located.

The period from January through April is the dry season, with the first three months in all cases having less than an inch of rainfall per month. In April, there were irregular rains totalling 1.29 to 2.07 inches for the month. These figures may be contrasted with the data presented by Bates, 1945, for the Villavicencio area where the dry season falls at about the same time of year, but is not nearly so extreme, or so long, with from three to more than eight inches of rainfall during the dry season months of January through March. In our area, the rainy season became established in May, with the remainder of the year characterized by abundant rainfall.

In Table I are also recorded the mean air temperatures and the mean relative humidities. The highest mean temperature was recorded at the end of the dry season in April, 82.8°F., and the lowest toward the end of the rains in October, November and December, 78.2 to 78.6°F. The lowest mean relative humidities are in the dry season at the beginning of the year, 70.0 to 76.5 per cent, and the highest in November, 90.6 per cent, near the end of the rainy season. Wind velocities are given for both the Atlantic and Pacific sides of the Isthmus to show that consistently higher winds are recorded from the Atlantic side. The winds are strongest during the dry season months of January through April, with 16.4 mph on the Atlantic side, and 10.2 mph on the Pacific side.

THE DISTRIBUTION OF THE SPECIES OCCURRING IN THE AREA

We were first concerned with the collection and identification of an adequate sample of the mosquitoes which attack man in the sylvan situation, at a variety of elevations, from sea-level to ridge-top, and from low rainfall area to high rainfall area. Since the number of human yellow fever cases was very few (less than ten), and no mouse protection test surveys of possible reservoir animals (in the main various species of primates) were available at the time of the initiation of the study, it seemed desirable to explore as many diverse habitats as possible, so that we might have information on the distribution and ecology of the sylvan mosquitoes in anticipation of later work on the distribution of the yellow fever virus in the human and animal population. It was also necessary to work out characters suitable for the identification of adult female mosquitoes, which would enable us to readily determine the large numbers of mosquitoes necessary for a comprehensive study of epidemiological significance. This phase of the work presented a problem in itself since certain of the groups involved, such as *Haemagogus*, are provided with but scant morphological characters by which the adult females may be differentiated. Our review of the field characters of particu-

TABLE I

Meteorological data, 1949

	JAN.	FEB.	MAR.	APR.	MAY	JUN.	JUL.	AUG.	SEP.	OCT.	NOV.	DEC.	YEAR TOTAL	NO. OF DAYS OF RAIN
Rainfall in Inches														
Balboa Heights...	.15	T	.26	2.10	8.74	7.71	6.70	8.09	6.06	11.68	10.05	6.93	68.48	186
El Jefe...........	.66	.91	.65	1.29	21.92	20.78	15.41	20.97	26.54	22.77	22.71	8.06	162.69	295
Madden Dam.....	.16	.12	.03	1.88	8.74	18.80	8.35	10.09	5.96	15.53	14.08	4.45	88.19	206
Cristobal.........	.88	.32	.48	2.07	11.23	12.72	12.61	15.60	9.64	17.72	36.65	15.86	135.78	241
Mean Air Temperature, Degrees Farenheit														
Balboa Heights...	79.2	80.8	81.7	82.8	81.1	79.4	80.2	80.2	79.4	78.5	78.2	78.6	80	
Mean Relative Humidity (Bihourly Mean), Per Cent														
Balboa Heights...	76.5	73.5	70.0	76.5	86.2	88.8	87.6	88.3	87.8	89.8	90.6	87.0	83.6	
Mean Wind Velocity, Miles Per Hour														
Balboa Heights...	7.3	10.2	9.9	7.6	5.3	4.1	4.8	4.8	4.9	4.7	5.5	5.0	6.2	
Cristobal.........	14.8	16.4	13.9	12.2	8.1	5.9	7.5	6.7	5.6	5.9	7.3	8.9	9.4	

lar use in the separation of the species of difficult groups will be published separately. It must be sufficient for the present to say that we are confident that we have been able to differentiate the species which do occur in the study areas in terms of the currently recognized nomenclatorial entities.

Tables II and III provide a summary of all the female mosquitoes caught and identified at the six principal stations which were operated throughout the year period, and Table IV the data from the supplementary stations H and J. Occasional male mosquitoes which were taken by the field collectors are excluded from these tables. In Table II the letter followed by a numeral indicates the station together with the height above the ground at which the collections were made, expressed in feet. The actual number of hours during which collections were made at each station and platform are indicated. In all, 29,271 mosquitoes were collected during 3,421 hours at the stations A to F, while another 6,729 mosquitoes were taken at stations H and J during 1,938 hours of collecting, and an additional 2,177 were taken during 146 hours of collecting at station K. These tables, as well as certain of the subsequent ones, record the sub-totals for all *Haemagogus* aside from the sub-totals given for all species of the tribe Culicini, since this genus is of special interest in connection with the transmission of sylvan yellow fever.

At the forest stations, four species of *Haemagogus* were taken as follows: *H. equinus*, *H. lucifer*, *H. spegazzinii falco*, and *H. chalcospilans*. *Haemagogus chalcospilans*, which is represented by only a single specimen in the collections from the forest stations, was taken abundantly attacking man in the coastal mangrove swamp at station G. In addition, *H. argyromeris* was found to be an abundant species attacking man on the ground in the open and in sparse secondary growth at station K. At the forest stations operated throughout the year, the most abundant species of this genus was *H. equinus* with 2,370 specimens taken, while *H. lucifer* followed with 1,470. At certain stations and platforms, however, *H. equinus* was outnumbered by *H. lucifer*, and at both stations B and C the combined total number of *H. lucifer* taken at all levels exceeded that for *H. equinus*. At stations H and J, *H. lucifer* also consistently outnumbered *H. equinus*, but these stations were operated only during the last part of the rainy season when, as will be shown later in the discussion of the seasonal distribution of the catches, *H. lucifer* predominated over *H. equinus* at the other forest stations as well. The total number of *H. spegazzinii falco* at all the forest stations was very much less than that of the two species just discussed. At the stations operated throughout the year, only 351 were taken, while stations H and J produced 491. At no station or platform did the number of this species approach the other two, excepting station J-3 where *H. spegazzinii falco* exceeded in number the combined total of the other two species. By contrast, in other endemic centers of sylvan yellow fever, in Brazil (Laemmert, Ferreira and Taylor, 1946 and Causey and Dos Santos, 1949) and in Colombia (Bates, 1944)[5] *H. spegazzinii falco* has been reported as the dominant or the only species found.

The data from the J stations are of special interest in that they demonstrate that the species of *Haemagogus* may be very local in their distribution. These six stations were located in a continuous forest, apparently uniform in character. Yet there was a very considerable variation in the proportions of the three *Haemagogus* taken in the forest canopy there, as will be seen by reference to Table IV. Thus stations J-3 and J-4 were located within 150 yards of one another, yet at station J-3 the number of *H. spegazzinii falco* taken exceeded *H. equinus* and *H. lucifer* combined, while at station J-4 the number of *H. lucifer* exceeded the combined total of *H. equinus* and *H. spegazzinii falco*.

As we noted above, *H. argyromeris* was at no time taken in the forest although it proved to be abundant in the open and in sparse secondary growth on

[5] The mosquito for which Bates and other authors working in Colombia used the then current name *Haemagogus capricornii* is according to the later taxonomic work of Kumm, Osorno, and Boshell, 1946, in fact *H. spegazzinii falco*, and we will thus refer to it throughout this paper.

Flamenco Island near the Pacific entrance to the Canal, and we have also taken it both breeding and feeding on man, in the outskirts of Panama City. This species is morphologically very close to *H. lucifer*, and while we have taken larvae (which were identified by rearing males) in water-filled bamboo-sections set out at stations A and B, which are in the forest, but closely adjoining cleared fields, adults were never taken biting there. From this evidence we conclude that *H. argyromeris* is essentially a species of open and sparsely vegetated areas, and while it will bite man in these situations, it does not invade the forest to bite, in contrast to *H. lucifer* which seems to replace it in the deep forest. A further explanation of the abundant biting by *H. argyromeris* at Flamenco Island, may be that since this is a small and somewhat barren island, man is one of the few sources of blood meals, contrasted with the diverse wild animal fauna available in the forest: i.e., *H. argyromeris* bites man only in the absence of other preferred hosts. While *H. lucifer* occurs exclusively in the deep forest on the Pacific side of the Isthmus, it is also found in open situations on the Atlantic side, breeding in tin cans, coconut husks, old tires, etc., in and about towns. This may be due to the higher rainfall on that side of the Isthmus.

The lack of biting by *H. argyromeris* in the forest, and the restriction of biting by *H. chalcospilans* to coastal mangrove swamps would seem to disqualify these two species as possible vectors of sylvan yellow fever in this area.

Considering the *Aedes*, we find that our collections produced members of three subgenera of this large and diverse genus. Of the subgenus *Finlaya*[6] we took four species, *A. leucocelaenus*, *A. leucotaeniatus*, *A. terrens* and *A. fluviatilis*. Certain taxonomic difficulties arose in the course of this study in the differentiation of female *A. leucocelaenus* and *A. leucotaeniatus*, but these were resolved, and we believe our tabulations of these two species are correct.[7] The purely taxonomic problem will be treated in a separate paper. At the stations operated throughout the year (Tables II and III) 399 specimens of *A. leucocelaenus* were taken, while *A. leucotaeniatus* with 37 specimens, *A. terrens* with 25 specimens and *A. fluviatilis* with 2 specimens were relatively uncommon. At the H and J stations (Table IV) an additional 635 specimens of *A. leucocelaenus* were taken while the other *Finlaya* were insignificant in numbers. *Aedes leucocelaenus* is a proven vector of yellow fever in South America, and indeed, the recent work of Waddell, 1949, indicates that it is an even more efficient vector of the virus than *A. aegypti*. It is significant that, like *H. spegazzinii falco*, this species was most abundant at stations B and C and the H and J stations. It will be recalled that station B was located close by the site where one of the first sylvan yellow fever cases occurred in the recent outbreak. The J stations

[6] Vargas, 1949, has revalidated the subgenus *Gualteria* Lutz to include all the American species of *Aedes* formerly placed in the subgenus *Finlaya* Theobald, as he believes that the latter subgenus is exclusively Oriental in distribution. As we have not had opportunity to critically read Vargas' paper we here use the name *Finlaya* in the sense of Edwards, 1932.

[7] Since this paper went to press we have obtained associated material for *Aedes leucocelaenus* from Brazil. A comparison of our Panama material with the Brazil specimens shows that we are dealing with a different and undescribed species closely related to *A. leucoceleanus*. A note on the *A. leucocelaenus* complex is now being prepared for publication.

TABLE II

Summary of female mosquitoes catches from tree stations during a one year period

Station Designation	A-0	A-20	A-40	B-0	B-23	B-46	C-0	C-44	C-71	D-0	D-26	D-48	E-0	E-28	E-46	F-0	F-26	F-45	Total
Number of Man Hours Collecting	206.5	206.5	207.5	245.5	243.5	244.0	224.5	226.0	227.0	215.0	210.5	210.5	66.5	66.5	66.5	186.5	183.0	185.0	3,421.0
Tribe Culicini																			
Haemagogus equinus	39	147	199	100	235	177	95	196	113	69	132	103	146	252	328	6	12	10	2,370
Haemagogus lucifer	15	22	52	102	146	288	185	157	177	20	17	23	56	58	114	6	18	15	1,470
Haemagogus spegazzinii falco	1			10	30	104	45	72	63	6	5	7	3		5				351
Haemagogus chalcospilans												1							1
Total Haemagogus	55	169	251	212	411	569	328	425	353	95	154	134	204	320	447	12	30	25	4,192
Aedes leucocelaenus	1			78	46	24	58	57	30	11	3	1	18	25	44	1		2	399
Aedes leucotaeniatus		1		2	1		8	8	3	10	2	1		1					37
Aedes terrens	3		8	6			5			3									25
Aedes fluviatilis				2															2
Aedes fulvus	30	1											16				1		48
Aedes serratus	1760	130	85	8									18			60	2		2,063
Aedes hastatus	14																		14
Aedes angustivittatus	250	12	4	0			1			1			4		1	1			289
Aedes euplocamus				2						1									3
Aedes taeniorhynchus	1182	14	1	384	1	1	130			9	2		351	1	1	11	9		2,097
Aedes septemstriatus				7			1	1							1				10
Aedes sp.			1						1										2
Psorophora cilipes	1																		1
Psorophora ferox	1878	459	653	37	3		1						5		1	75	13	8	3,133
Psorophora lutzii	54	43	48	9			2	2	5			3	96	20	17	66	42	21	428
Psorophora champerico	6																		6
Psorophora cingulata										3						1			4
Taeniorhynchus pseudotitillans	3																		3
Taeniorhynchus titillans	802	59	48	1442	53	6	261	4		152	1		3			1474	380	153	4,838
Taeniorhynchus indubitans	1	9	1													5			16
Taeniorhynchus fasciolata	1738	360	144	37						2						390	16	6	2,693
Taeniorhynchus nigricans																4908	347	141	5,396
Taeniorhynchus sp.	5																		5
Culex corniger	1																		1
Culex mollis							2			1									3
Culex (Culex) sp.	1			1												3	1		6

Culex (Melanoconion) sp.				1												1			2
Culex (Isostomyia) sp.													2						2
Culex sp.		1	2							8	1								12
Orthopodomyia fascipes						1	1												2
Total Culicini	7791	1258	1246	2237	515	601	796	497	392	296	163	139	717	367	512	7008	841	356	25,732
Tribe Sabethini																			
Trichoprosopon digitatum				11	1		2	1					1						16
Trichoprosopon espini	70	32	46	1															149
Trichoprosopon magnum					2	1				1	1	3							8
Trichoprosopon longipes	8			20	3	1							2						34
Trichoprosopon lampropus							1												1
Trichoprosopon sp.	64	64	37	44		2	1	1	1			1				7		1	223
Wyeomyia melanopus										1									1
Wyeomyia celaenocephala	5	1	1	39	7	7	10												70
Wyeomyia arthrostigma		1																	1
Wyeomyia hemisagnosta				7			4	1	1	2	1	3							19
Wyeomyia (Wyeomyia) n. sp.					1			1	2			5							9
Wyeomyia (Wyeomyia) sp.*	199	41	28	78	28	17	12	1	1	7	5	1	9		2	110	11	4	554
Wyeomyia ypsipola	1																		1
Wyeomyia personata	1	5		9	1		1			2	1								20
Wyeomyia melanocephala	2			6									1						9
Wyeomyia circumcincta	1																		1
Wyeomyia chalcocephala													2						2
Wyeomyia clasoleuca							1												1
Wyeomyia jocosa†										2									2
Wyeomyia prolepidis				2															2
Wyeomyia (Dendromyia) sp.	76	4	32	21	1	2	3	1		3					1	24	3	2	173
Limatus durhamii	4			6								1							11
Limatus asulleptus	1			4						2	1					1			9
Sabethes tarsopus			1	5	8	21		10	17		2	1	1	5	7			1	79
Sabethes cyaneus	9	4	5	20	44	31	3	3	3	3	4	13	2	5	1				150
Sabethes (Sabethes) sp.					4	2							1				2		9
Sabethes chloropterus	8	19	44	58	281	322	52	279	200	21	40	94	5	35	78	7	9	19	1,572
Total Sabethini	449	171	194	331	381	406	90	298	225	44	55	122	24	45	89	149	25	27	3,126
Tribe Anophelini																			
Chagasia bathanus				1	3	4			2				1		1			1	13
Anopheles kompi										1									1
Anopheles eiseni				1			4			1			30	3	2				41

TABLE II—*Continued*

Station Designation	A-0	A-20	A-40	B-0	B-23	B-46	C-0	C-44	C-71	D-0	D-26	D-48	E-0	E-28	E-40	F-0	F-26	F-45	Total
Number of Man Hours Collecting	206.5	206.5	207.5	245.5	243.5	244.0	224.5	226.0	227.0	215.0	210.5	210.5	66.5	66.5	68.5	186.5	183.0	135.0	3,421.0
Tribe Anophelini—*Continued*																			
Anopheles pseudopunctipennis				2															2
Anopheles apicimacula				1									1						2
Anopheles punctimacula	1		1	4									5			13	1		25
Anopheles albimanus	2															31		1	34
Anopheles triannulatus																29	3		32
Anopheles aquasalis													8						8
Anopheles oswaldoi													2						2
Anopheles (Nyssorhynchus) sp.	7												7	1		224	3	5	247
Anopheles neivai					1		1						2	1	1				6
Total Anophelini	10	0	1	9	4	4	5	0	2	2	0		56	5	4	297	7	7	413
Total All Species	8250	1429	1441	2577	900	1011	891	795	619	342	218	261	797	418	605	7454	873	390	20,271

* *Wyeomyia (Wyeomyia)* sp. includes mostly specimens of *Wyeomyia mitchellii* Theobald and *Wyeomyia scotinomus* D. and K., which in most cases could not be separated to species due to the rubbed condition of the tarsi.

† This is the species referred to by Dyar, 1928, and Lane and Cerqueira, 1942, as *Wyeomyia complosa* Dyar. A further note on the synonymy of this group will be published later.

TABLE III

Combined totals of all female mosquitoes captured at tree stations during a year period

Station Designation	A	B	C	D	E	F	Total
Number of Man Hours Collecting	620.5	733.0	677.5	636.0	199.5	554.5	3620.5
Tribe Culicini							
Haemagogus equinus	385	512	405	304	736	28	2,370
Haemagogus lucifer	89	536	519	60	227	39	1,470
Haemagogus spegazzinii falco	1	144	180	18	8		351
Haemagogus chalcospilans				1			1
Total Haemagogus	475	1192	1104	383	971	67	4,192
Aedes leucocelaenus	1	148	145	15	87	3	399
Aedes leucotaeniatus	1	3	19	13	1		37
Aedes terrens	11	6	5	3			25
Aedes taeniorhynchus	1197	386	130	11	353	20	2,097
Aedes serratus	1975	8			18	62	2,063
Aedes septemstriatus		7	2		1		10
Aedes sp.	318	13	2	2	21	2	358
Psorophora ferox	2990	40	1		6	96	3,133
Psorophora lutzii	145	9	9	3	133	129	428
Psorophora sp.	7			3		1	11
Taeniorhynchus titillans	909	1501	265	153	3	2007	4,838
Taeniorhynchus fasciolata	2242	37		2		412	2,693
Taeniorhynchus nigricans						5396	5,396
Taeniorhynchus sp.	19					5	24
Culex sp.	5	2	2	10	2	5	26
Orthopodomyia fascipes		1	1				2
Total Culicini	10295	3353	1685	598	1596	8205	25,732
Tribe Sabethini							
Trichoprosopon sp.	321	86	7	6	3	8	431
Wyeomyia (Wyeomyia) sp.	276	184	33	25	11	125	654
Wyeomyia (Dendromyia) sp.	122	42	6	8	4	29	211
Limatus sp.	5	10		4		1	20
Sabethes cyaneus	18	95	9	20	8		150
Sabethes tarsopus	1	34	27	3	13	1	79
Sabethes (Sabethes) sp.		6			1	2	9
Sabethes chloropterus	71	661	531	155	119	35	1,572
Total Sabethini	814	1118	613	221	159	201	3,126
Tribe Anophelini	11	17	7	2	65	311	413
Total All Mosquitoes	11120	4488	2305	821	1820	8717	29,271

are close to stations B and C, and the H stations are near the locality at which a later case of yellow fever occurred. Whether by coincidence or not, this species was most prevalent in our study in the areas associated with known yellow fever fatalities.

Captures of mosquitoes of the aedine subgenus *Ochlerotatus* at the stations where year-long observations were made, were dominated by the two species *A. serratus* with 2,063 specimens and *A. taeniorhynchus* with 2,097 specimens, while *A. angustivittatus* followed with 289 specimens. The other species of this subgenus,

TABLE IV

Summary of total catches of mosquitoes at stations H and J

Station Designation	H-1	H-2	H-3	H-4	J-1	J-2	J-3	J-4	J-5	J-6	Total
No. of Man Hours	179	226	225	94	272	267	206	213	129	127	1938
No. of Days	26	34	34	14	39	38	31	32	18	18	284
Tribe Culicini											
Haemagogus equinus	190	76	130	20	50	69	17	51	138	72	813
Haemagogus lucifer	773	363	591	147	326	210	48	103	139	189	2,889
Haemagogus spegazzinii falco	64	52	27	6	83	95	77	28	26	33	491
Total Haemagogus	1027	491	748	173	459	374	142	182	303	294	4,193
Aedes leucocelaenus	43	35	29	12	113	101	33	84	52	133	635
Aedes leucotaeniatus	2	3	4	1	5	1		1			17
Aedes terrens	1							1			2
Aedes fluviatilis										1	1
Aedes euplocamus										1	1
Aedes septemstriatus									1	1	2
Psorophora ferox		1							1		2
Psorophora lutzii	9	7	7	1		1					25
Psorophora cingulata										1	1
Taeniorhynchus titillans	2	2	1		4	1	4	2		2	18
Taeniorhynchus fasciolata	1	1									2
Taeniorhynchus nigricans	5	2	2								9
Taeniorhynchus indubitans	7	1	2				2		1		13
Taeniorhynchus sp.					1						1
Culex sp.									1	1	2
Total Culicini	1097	543	793	187	582	478	181	270	359	434	4,924
Tribe Sabethini											
Trichoprosopon sp.	6		1			2			18	3	30
Wyeomyia (Wyeomyia) sp.	98	21	19		34	45	51	20	33	8	329
Wyeomyia (Dendromyia) sp.		1	2		4		3	1	2		13
Sabethes cyaneus	19		21		12	22	40	2	20	2	138
Sabethes tarsopus	145	46	88		10	18	11	2	9	5	334
Sabethes chloropterus	110	80	149	14	126	125	42	114	84	110	954
Total Sabethini	378	148	280	14	186	212	147	139	166	128	1,798
Tribe Anophelini											
Anopheles punctimacula							1				1
Chagasia bathanus	3		1			1				1	6
Total Anophelini	3	0	1	0	0	1	1	0	0	1	7
Total all mosquitoes	1478	691	1074	201	768	691	329	409	525	563	6,729

A. fulvus, *A. hastatus* and *A. euplocamus* were present in only insignificant numbers. It will be noted that *A. serratus* was almost entirely confined to the coastal sea-level stations A and E, with only a few other specimens taken at station F on the Chagres River. *A. taeniorhynchus* was also largely confined to the low altitude coastal stations, but probably as an expression of the very considerable flight range of this species from its coastal breeding places, it did invade the forest in decreasing numbers at successively higher elevations, so that a few specimens, 11 in number, were even taken at station D at an elevation of 2100 feet.

The aedine subgenus *Howardina* was represented by a single species, *A. septemstriatus* with a few specimens taken at scattered stations.

All three subgenera of *Psorophora* were taken. *Psorophora* (*Psorophora*) *cilipes*, and *P.* (*Grabhamia*) *cingulata*, were insignificant in numbers. The dominant subgenus was *Janthinosoma*. At the principal stations shown in Tables II and III, Psorophora (*Janthinosoma*) *ferox*, with 3,133 specimens, was the most abundant representative of the genus, with the main catches being from the coastal sea-level station A, and lesser numbers at station F on the Chagres River and station B at 400 feet in elevation. None were taken at station D at 2100 feet. *Psorophora* (*Janthinosoma*) *lutzii* was next in abundance with 428 specimens, and showed a somewhat more uniform distribution at the various stations including even 3 specimens from the 2100 foot station D. *Psorophora* (*Janthinosoma*) *champerico*, the third representative of this subgenus, was rare, with only 6 specimens taken, these at station A.

The genus *Taeniorhynchus*[8] was represented by two subgenera, each including large elements of the mosquito fauna collected at the principal stations. In the subgenus *Taeniorhynchus*, the species *titillans* was extremely common with 4,838 specimens taken. Almost half of this number were taken at station F on the Chagres River where the species breeds in great abundance. On the Pacific slope stations, A, B, C, and D, decreasing numbers were taken at successively higher elevations. Only at station E, on the Atlantic side, was the species rare. The separation of females of *T. titillans* and *T. indubitans* requires special preparation of the terminal segments of the abdomen for certain identification and, as this species was not of special interest in this study, time to accomplish this was, in general, not taken. The number of *T. indubitans* reported here is, therefore, lower than the actual number present, some having been included with *T. titillans*. *T. pseudotitillans*, the third representative of the subgenus *Taeniorhynchus*, has not previously been reported from Panama and we took only 3 specimens, all at station A.

The subgenus *Rhynchotaenia* was represented by two species, *T. fasciolata* with 2,693 specimens, and *T. nigricans* with 5,396 specimens, at the principal stations. The bulk of the *T. fasciolata* were from the Pacific coastal station A, with the Chagres River station F being second in importance. The species was

[8] The use of the generic name *Taeniorhynchus* Lynch-Arribálzaga, 1891, versus *Mansonia* Blanchard, 1901, has been the subject of much dispute. The authors, unaware of any ruling by the International Commission on Zoological Nomenclature on this matter, have adopted the name *Taeniorhynchus* following Edwards, 1941, who submitted the question to the Nomenclature Committee of the Royal Entomological Society of London and the Secretary of the International Commission on Zoological Nomenclature, who "—expressed a unanimous opinion in favor of the use of the name *Taeniorhynchus* rather than *Mansonia* for this genus".

rare at the elevated forest stations and was not taken at the Atlantic coastal station E. *T. nigricans*, the most abundant of all the mosquito species taken, was wholly confined to the Chagres River station F, except for a few specimens from the H stations.

Of the genus *Culex*, three subgenera were represented as follows, *Culex* (*Culex*), *Culex* (*Melanoconion*), and *Culex* (*Isostomyia*). These were all insignificant in numbers, there being only 26 specimens of the genus at the principal stations and an additional 2 at the J stations.

Orthopodomyia fascipes is recorded only twice.

The tribe Sabethini was represented by a considerable diversity of species, but only one species, *Sabethes chloropterus*, was present in significant numbers at the principal stations, although there were moderate numbers of *S. tarsopus* and *S. cyaneus* at the supplementary stations H and J. We have, in general, followed the monograph of Lane and Cerqueira, 1942, on the American Sabethini, for the names we have used.

Of the genus *Trichoprosopon* at the principal stations, 431 specimens were taken in all, including the five species *T. digitatum*, *T. espini*, *T. magnum*, *T. longipes* and *T. lampropus*, and a number of specimens which were not identified as to species. Of those specifically identified, *T. espini*, with 149 specimens, was the most abundant, and all but one of these were taken at station A. The species *T. digitatum* and *T. longipes* were taken largely at station B, while *T. magnum* was the predominant species at station D.

The genus *Wyeomyia* was represented by the greatest diversity of species of any of the genera taken during this study. As the mosquitoes of this genus are difficult to determine as females, and the genus has not seemed relevant in the transmission of yellow fever, the bulk of the material was determined only as far as subgenus. The subgenus *Wyeomyia* is represented by the seven species *W. melanopus*, *W. celaenocephala*, *W. arthrostigma*, *W. hemisagnosta* a new species close to *W. hemisagnosta*, all of which are included in Table II, and two other species, *W. mitchellii* and *W. scotinomus* which are lumped under *Wyeomyia* (*Wyeomyia*) sp. These two could only occasionally be determined to species, when the specimens were in excellent condition, without rubbed scales. Of the *Wyeomyia* (*Wyeomyia*) which were specifically determined, *W. celaenocephala*, with 70 specimens, was the most abundant species, these all being taken at stations A, B, and C. The subgenus *Dendromyia* included eight species. Of those which were identified to species, *W. personata*, with 20 specimens, was the most abundant.

The genus *Limatus* is represented by the two species *L. durhamii* and *L. asulleptus* with a total of only 20 specimens.

Representatives of two subgenera of *Sabethes* were taken, *S.* (*Sabethes*) and *S.* (*Sabethoides*). Of the subgenus *Sabethes* at the principal stations, *S. cyaneus* with 150 specimens was about twice as abundant as *S. tarsopus* with 79 specimens; but at the H and J stations, operated only during the latter part of the rainy season, the converse was true with the collections totalling 138 *S. cyaneus* and 334 *S. tarsopus*. *Sabethes chloropterus*, of the subgenus *Sabethoides*, was the most abundant sabethine mosquito taken, with 1,572 being the total number collected at all the stations operated throughout the year, and an additional 954 from the H and J stations. This species was most abundant at station B, where 661 specimens were captured, and next in abundance at station C, where 531 were taken, while significant numbers were also collected at the J stations in the same general area. One is struck at once by the fact that the occurrence of this mosquito in our study area is very similar to that of the two proven South American vectors of sylvan yellow fever, *Haemagogus spegazzinii falco* and *Aedes leucocelaenus*, encountered in the study. It is further significant that a member of the subgenus *Sabethoides* was included in the pool of wild-caught mosquitoes which was found to be positive for yellow fever virus by Shannon, Whitman, and Franca, 1938, after the intercerebral inoculation into mice of a suspension of triturated sabethine mosquitoes. At station B, close by a fatal case of sylvan yellow fever, *S.* (*Sabethoides*) *chloropterus* was about four times as abundant as either *H. spegazzinii falco* or *A. leucocelaenus*, and it even outnumbered here the two common *Haemagogus*, *H. equinus* and *H. lucifer*. We unfortunately do not know of any laboratory experiments to establish the efficiency of this species as a yellow fever vector, but this is a possibility which should be explored.

The tribe Anophelini is represented by a surprising diversity of species, considering that all our catches were made in the daytime. Two genera, *Chagasia*, and *Anopheles*, were taken. In the genus *Anopheles*, the subgenera *Stethomyia* with species *kompi*; *Anopheles*, with species *pseudopunctipennis*, *apicimacula*, and *punctimacula*; *Nyssorhynchus* with species *albimanus*, *triannulatus*, *aquasalis*, and *oswaldoi*; and *Kerteszia* with the species *neivai*, were taken. In terms of numbers, the anophelines were abundant at station F, on the Chagres River, where there is heavy production of the two *Nyssorhynchus*, *A. albimanus* and *A. triannulatus*. In general, no attempt was made to separate these two closely similar species. The greatest diversity of species was obtained at station E, on the Caribbean side of the Isthmus, where at least seven anophelines were taken, followed by station B, where five were taken.

THE ANNUAL CYCLE OF ABUNDANCE

In Tables V to X are recorded the captures of mosquitoes per ten man hours by months. Although these stations were actually operated on a weekly basis, we find that a consolidation of the data by months does not obscure the essential facts regarding the fluctuations in abundance of the species. All these tables cover the year period from February 1949 through January 1950 except Table IX for station E. The platforms at this station were not completed, so field observations could not commence, until the beginning of March 1949. This station was therefore operated through the month of February 1950, to complete the year cycle there. During the month of November 1949 unavoidable circumstances occurred which permitted the operation of this station only once, and this month is therefore, omitted from the summary for this station. As there were occasional interruptions in the routine of the collecting at the stations due to heavy rain, or other circumstances, the records of the catches were all reduced

TABLE V

The annual cycle of diurnal mosquitoes attacking man in the forest, per ten man hours, by months

Station A

	Feb. 1949			Mar. 1949			Apr. 1949			May 1949			Jun. 1949			Jul. 1949			Aug. 1949			Sept. 1949			Oct. 1949			Nov. 1949			Dec. 1949			Jan. 1950		
	Station Designation																																			
	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40	A 0	A 20	A 40
Tribe Culicini																																				
Haemagogus equinis							2			4	21	30	5	14	22	8	28	30	2	7	15		3	7	2	2	3	x	9	8		1				
Haemagogus lucifer											2	2	2	x	5	3	4	12			3	2	1	2		4	3	4	6	6						
Haemagogus spegazzinii falco																												x								
Total Haemagogus	0	0	0	0	0	0	2	0	0	4	23	32	8	15	27	11	32	42	2	7	18	2	4	9	2	6	6	5	15	14	0	1	0	0	0	0
Aedes leucocelaenus																												x								
Aedes leucotaeniatus																										x										
Aedes terrens													1															x								
Aedes serratus										5			199	11	4	175	4	2	219	16	3	133	17	21	174	14	8	132	14	10	47	5	8			
Aedes taeniorhynchus				x			129			246	x		248	8	5	8			4																	
Aedes (Ochlerotatus) sp.	x						x			20			72	4	2	25	x		35	x	1	16	x		4			2			1	1				
Psorophora cilipes																						x														
Psorphora ferox							x			44	2	6	407	99	139	238	31	33	105		48	75	44	104	179	46	47	86	20	29	25	4	1	1		
Psorophora lutzii										5	2	4	23	19	16	2	x		x	x	5	x	x	2	1	1						x	x			
Psorophora champerico																4																				
Taeniorhynchus pseudotitillans	1			x																																
Taeniorhynchus titillans	216	x	x	38			1			10			2			6	x	x	22	3	1	15	3	3		2	3	19	16	8	22	16	10	65	1	5
Taeniorhynchus indubitans																				1			4	x												
Taeniorhynchus fasciolata	41			10						x			3	1	x	2	x		55	2	6	125	16	4	374	97	24	228	63	14	197	53	40	38	3	4
Taeniorhynchus nigricans																			7																	
Taeniorhynchus sp.	3																																			
Culex sp.										x						x					x		x	x												
Total Culicini	262	x	x	49	0	0	133	0	0	335	23	41	964	157	194	471	70	78	449	68	83	357	92	144	745	166	89	474	128	76	293	82	61	105	4	8
Tribe Sabethini																																				
Trichoprosopon sp.										2			2	1		4	2	1	21	5	12	18	13	15	6	15	7	23	27	15	15	3	2			
Wyeomyia (Wyeomyia) sp.							2			3	x		14	x	2	30	2	x	23	5	2	13	7	2	27	7	8	9	4	1	5					
Wyeomyia (Dendromyia) sp.													1						x			x			19	4	11	26	2		2					

Limatus sp.										x			1			2									1						1					
Sabethes (Sabethes) sp.				x							x										1			2		x		2	2	x				x		
Sabethes chloropterus	x					1		x				x		1	2		3	7	x	1	7	4	2	3		2	2	x	3	2			1			
Total Sabethini	x	0	0	x	0	1	2	x	0	6	x	x	19	3	4	35	7	9	44	11	22	35	23	22	54	28	28	61	37	28	24	3	4	x	0	0
Tribe Anophelini	2	0	0	1	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	x	x	0	0	1	0	0	x	0	0
Total all Species	264	x	x	51	0	1	134	x	0	341	29	42	983	160	198	506	77	88	494	79	106	402	115	165	799	193	117	536	164	104	318	85	64	106	4	8

"x" indicates less than 1 mosquito per 10 man hours.

TABLE VI

The Annual cycle of diurnal mosquitoes attacking man in the forest, per ten man hours, by months

Station B

	Feb. 1949			Mar. 1949			Apr. 1949			May 1949			Jun. 1949			Jul. 1949			Aug. 1949			Sept. 1949			Oct. 1949			Nov. 1949			Dec. 1949			Jan. 1950		
STATION DESIGNATION	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46	B 0	B 23	B 46
Tribe Culicini																																				
Haemagogus equinus		2						x		6	12	12	15	41	33	9	31	25	5	8	6	7	7	8	2	8	3	6	15	6		2	2	1	x	x
Haemagogus lucifer								x		2	2	3	6	10	21	11	15	25	2	4	16	9	4	17	7	11	21	8	20	27	4	3	11	x	2	x
Haemagogus spegazzinii falco													3	5	15	x	2	16	x	x	2	x	3	6		3	5	x	1	8			4		x	x
Total Haemagogus	0	2	0	0	0	0	0	1	0	8	14	15	25	56	68	21	49	67	7	12	23	16	14	31	9	21	30	15	35	41	4	4	17	2	3	2
Aedes leucocelaenus													2	2	x	2	2	2	3	1	x	6	4	2	9	4	3	12	6	2	2	3	2	x		
Aedes leucotaeniatus																									x				x							
Aedes terrens																						2			x			x								
Aedes serratus													2			1			x															x		
Aedes taeniorhynchus							53			127		x	10	x																						
Aedes septemstriatus	x									x			1			x			x															x		
Aedes (Ochlerotatus) sp.							1			3			x			x																				
Psorophora ferox							6	x		4			5	1		x			x			x			x						1			x		
Psorophora lutzii										3			1																							
Taeniorhynchus titillans	228	x		46			8			3			x			1			5	x		8			3			7			56	2	2	344	19	1
Taeniorhynchus fasciolata																			1			4			2			4			5			4		
Culex sp.	x																											x								
Orthopodomyia fascipes												x																								
Total Culicini	230	2	0	46	0	0	68	2	0	151	14	16	47	61	69	27	51	69	29	14	24	34	18	32	25	25	32	38	42	43	68	9	20	351	22	3
Tribe Sabethini																																				
Trichoprosopon sp.	x	2			x		1			1			x			4	x		1	x	x	4			x			7			13		1	5		
Wyeomyia (Wyeomyia) sp.	x	x		4	x	x	11	x		4	1	x	3	6	2	8	3	5	7	3	1	12	2	1	3		1	6	1	x	2	1		1	x	
Wyeomyia (Dendromyia) sp.							3						3			2			x	x		x			1		1	x			7	x		2		
Limatus sp.										1			2						x			1														
Sabethes (Sabethes) sp.	2	x	x	4	1		2	2	x		x	2			4		1	4	x	3	3	x	5	5		3	2	x	7	4	2	1	1	x	2	1
Sabethes chloropterus	2		x	1	2	2	3	5	2	x	2	8	3	15	35	2	28	32	2	38	39	8	15	14	2	8	8	3	15	15	2	2	6	1	4	4
Total Sabethini	5	6	2	8	5	2	20	7	3	7	4	11	13	21	41	15	33	41	12	45	44	26	21	20	7	12	12	17	24	20	25	5	8	9	6	6
Tribe Anophelini	0	0	0	0	0	0	2	0	x	x	0	0	x	0	0	0	0	0	x	x	0	0	x	0	0	0	x	x	0	x	x	x	x	x	x	0
Total All Species	234	12	2	54	5	2	89	9	3	159	19	27	61	82	110	42	84	109	31	59	68	59	40	52	31	37	44	56	66	64	93	14	28	360	29	9

"x" indicates less than 1 mosquito per 10 man hours.

TABLE VII

The annual cycle of biurnal mosquitoes attacking man in the forest, per ten men hours, by months

Station C

	Feb. 1949			Mar. 1949			Apr. 1949			May 1949			Jun. 1949			Jul. 1949			Aug. 1949			Sept. 1949			Oct. 1949			Nov. 1949			Dec. 1949			Jan. 1950		
	Station Designation																																			
	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71	C 0	C 44	C 71
Tribe Culicini																																				
Haemagogus equinus							4	2	4	1	8	7	22	53	31	3	18	5	2	4		5	5	5	x	3		3	1	x	3	2		x		
Haemagogus lucifer							1			17	7	14	21	17	12	18	21	29	8	9	9	12	15	12	5	2	3	6	8	10	13	5	4	2	x	x
Haemagogus spegazzinii falco											x		4	7	8	5	12	8		3	2	4	5	5	1	3	2	6	6	7	3	2	3			
Total Haemagogus	0	0	0	0	0	0	5	2	4	18	16	22	47	77	52	26	51	42	10	16	12	21	25	22	7	8	5	16	16	17	18	9	6	2	x	x
Aedes leucocelaenus											x	3	8	6	2	2	4	4	5	5	3	10	10	2	5	2	x	x	2				x	x	x	
Aedes leucotaeniatus										1	2		x	2	x							2	x	x	x									x		
Aedes terrens													x			2																				
Aedes taeniorhynchus							22			14			31																							
Aedes septemstriatus													x	x										x												
Aedes (Ochlerotatus) sp.										x																										
Psorophora ferox																															x					
Psorophora lutzii										x	1	3	x																							
Taeniorhynchus titillans	47			4			2			x						1															18			73	2	
Culex sp.													x			x																				
Orthopodomyia fascipes	x																																			
Total Culicini	48	0	0	4	0	0	29	2	4	35	19	28	88	85	54	31	55	46	15	21	15	34	36	25	13	10	6	17	18	17	36	9	7	77	3	x
Tribe Sabethini																																				
Trichoprosopon sp.							x							x														x	x		x		x			
Wyeomyia (Wyeomyia) sp.				1			2			2		x	3	x		3	x	x			x				2						x			x		
Wyeomyia (Dendromyia) sp.								x											x			1			x									x		
Sabethes (Sabethes) sp.			2			x				x	x	x		x	1	x	x	1		3	x		2	1			3		x				1	x		
Sabethes chloropterus	x	x		1	8	x	2	4	2	3	4	3	3	23	20	3	36	29	1	22	22	5	13	10	3	12	9	3	10	4	1	8	3	1	6	3
Total Sabethini	x	x	2	2	8	x	5	5	2	5	4	4	6	25	21	6	37	30	2	25	24	6	15	12	5	12	12	4	10	4	2	8	5	3	6	3
Tribe Anophelini	0	0	0	0	0	0	x	0	0	x	0	0	x	0	0	0	0	1	x	0	0	0	0	0	x	0	0	0	0	0	0	0	0	0	0	0
Total All Species	49	x	2	6	8	x	35	7	6	41	23	32	94	110	75	38	92	77	18	46	39	40	52	37	19	22	18	21	29	21	38	17	12	79	9	3

"x" indicates less than 1 mosquito per 10 man hours.

TABLE VIII

The annual cycle of diurnal mosquitoes attacking man in the forest, per ten man hours, by months

Station D

	Feb. 1949			Mar. 1949			Apr. 1949			May 1949			Jun. 1949			Jul. 1949		
Station Designation	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48
Tribe Culicini																		
Haemagogus equinus							3	6	2	8	23	16	22	38	35	1	2	3
Haemagogus lucifer										5	6	3	x	2	2	x		2
Haemagogus spegazzinii falco													x	2	2	2	1	1
Haemagoggus argyromeris																		
Total Haemagogus	0	0	0	0	0	0	3	6	2	13	28	19	23	42	39	4	3	6
Aedes leucocelaenus							1			2	x		2	1	x			
Aedes leucotaeniatus										4	x	x				2	x	
Aedes terrens																x		
Aedes taeniorhynchus							1			3			1	1				
Aedes (Ochlerotatus) sp.										x			x					
Psorphora lutzii												x			1			
Psorophora cingulata													x			x		
Taeniorhynchus titillans	12			x	x		3			x						x		
Taeniorhynchus fasciolata							x											
Culex sp.	6													x				
Total Culicini	18	0	0	x	x	0	8	6	2	23	29	21	27	45	41	8	4	6
Tribe Sabethini																		
Trichosposopon sp.							x					x					x	1
Wyeomyia (Wyeomyia) sp.							x			x		2	x		x	2	2	x
Wyeomyia (Dendromyia) sp.				x	x								x			x		
Limatus sp.													x		x	x		
Sabethes (Sabethes) sp.							1	1	x						2			1
Sabethes chloropterus							2	3	3	3	3	8	1	2	6	1	4	10
Total Sabethini	0	0	0	x	x	0	4	4	4	3	3	10	3	2	9	5	7	13
Tribe Anophelini	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total All Species	19	0	0	2	x	0	12	10	6	26	32	31	30	47	50	13	10	19

	Aug. 1949			Sept. 1949			Oct. 1949			Nov. 1949			Dec. 1949			Jan. 1950		
Station Designation	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48	D 0	D 26	D 48
Tribe Culicini																		
Haemagogus equinus	x	2		1	2	1	x	x				2	3	3	2			
Haemagogus lucifer	2	1	1	2	x	2			x		2	2	x		1			
Haemagogus spegazzinii falco				x		x			x									
Haemagoggus argyromeris			x															
Total Haemagogus	2	3	2	4	2	4	x	x	1	0	2	4	4	3	3	0	0	0
Aedes leucocelaenus				x									x					
Aedes leucotaeniatus	x																	
Aedes terrens													x					
Aedes taeniorhynchus																		
Aedes (Ochlerotatus) sp.																		
Psorphora lutzii																		
Psorophora cingulata				x														
Taeniorhynchus titillans				x									24			35		
Taeniorhynchus fasciolata							x											
Culex sp.																		
Total Culicini	3	3	2	6	2	4	1	x	1	0	2	4	28	3	3	35	0	0
Tribe Sabethini																		
Trichosposopon sp.															x			
Wyeomyia (Wyeomyia) sp.		x	2			x							x			x		
Wyeomyia (Dendromyia) sp.													1					
Limatus sp.				x	x													
Sabethes (Sabethes) sp.		x	1		x	x								x	2			
Sabethes chloropterus	x	5	10	2	2	8							1	2	5		1	1
Total Sabethini	x	6	13	2	3	9	0	0	0	0	0	0	4	2	8	x	1	1
Tribe Anophelini	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Total All Species	3	9	14	8	6	13	1	x	1	0	2	4	32	5	11	36	1	1

"x" indicates less than 1 mosquito per 10 man hours.

TABLE IX

The annual cycle of diurnal mosquitoes attacking man in the forest, per ten man hours, by months

Station E

	Mar. 1949			Apr. 1949			May 1949			Jun. 1949			Jul. 1949			Aug. 1949			Sept. 1949			Oct. 1949			Nov. 1949			Dec. 1949			Jan. 1950			Feb. 1950		
	STATION DESIGNATION																																			
	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46	E 0	E 28	E 46
Tribe Culicini																																				
Haemagogus equinus	3				2		93	105	193	112	244	192	6	30	60	2		5	3		9	4	2	24				2	22	22	16		9	7	11	13
Haemagogus lucifer							18	3	12	17	27	31	9	9	17	3	10	10	11	9	25	13	9	20				3	23	50	18	4	7	4	9	
Haemagogus spegazzinii falco							3			2		2						2						4												
Total Haemagogus	3	0	0	0	2	0	115	108	205	130	270	225	14	39	77	5	10	17	13	9	35	16	11	47				5	45	72	33	4	16	11	20	13
Aedes leucocelaenus								3		7	8	8		6	11		2	10	12	15	12	4	4	15				3		8	2					
Aedes terrens													1																							
Aedes serratus									2	22			6						1																	
Aedes taeniorhynchus				2			18	2	2	470			87																							
Aedes (Ochlerotatus) sp.									2	19			6																							
Psorophora ferox										8																										
Psorophora lutzii				53	7	2	108	25	23	11	3	3			1																					
Taeniorhynchus titillans										2									1															2		
Culex sp.				4																																
Total Culicini	3	0	0	60	9	2	242	138	233	668	252	236	114	44	90	5	12	27	28	24	47	20	15	62				8	45	80	36	4	16	13	20	13
Tribe Sabethini																																				
Trichoprosopon sp.										2						2			1																	
Wyeomyia (Wyeomyia) sp.							3			3		2	7		1																					
Wyeomyia (Dendromyia) sp.													3						1					2												
Sabethes (Sabethes) sp.	2										2	2		3	1	2		2	1	7			2					2		3			2			
Sabethes chloropterus	2		2					2	3		13	7		4	21		7	39		5	21	5	15	16					7	12	2				2	
Total Sabethini	3	0	2	0	0	0	3	2	3	5	15	10	10	7	24	3	7	40	4	12	21	5	16	18				2	7	15	2	0	2	0	2	0
Tribe Anophelini	13	0	0	4	0	0	7	0	0	11	0	0	14	1	0	0	2	0	1	0	0	0	0	4				0	0	0	2	0	0	47	4	4
Total All Species	20	0	2	64	9	2	252	140	236	685	297	246	138	53	114	8	20	67	33	36	68	25	31	84				10	52	95	40	4	18	60	27	18

"x" indicates less than 1 mosquito per 10 man hours.

TABLE X

The annual cycle of diurnal mosquitoes attacking man in the forest, per ten man hours, by months

Station F

	Feb. 1949			Mar. 1949			Apr. 1949			May 1949			Jun. 1949			Jul. 1949			Aug. 1949			Sept. 1949			Oct. 1949			Nov. 1949			Dec. 1949			Jan. 1950		
	Station Designation																																			
	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45	F 0	F 26	F 45
Tribe Culicini																																				
Haemagogus equinus										x	4	5	1	x		x	x	x			1	x			x				x							
Haemagogus lucifer											2	x	1		x	x	3	2		1			3	3	x		2		x		x	x				
Total Haemagogus	0	0	0	0	0	0	0	0	0	x	6	6	3	x	x	x	3	3	0	1	1	x	3	3	2	0	2	0	1	0	x	x	0	0	0	0
Aedes leucocelaenus															x													x					x			
Aedes serratus										2			21			9	x		5	1		2			x											
Aedes taeniorhynchus										8			2	7																						
Aedes (Ochlerotatus) sp.													x							1																
Psorophora ferox										4			13	2	2	8	2		20			1			2	x		3	1	1	3	x				
Psorophora lutzii							1			2			10	3	2	4	11	3	21	5	5	3	3	2	2	2	2	4	1		x					
Taeniorhynchus titillans	78	3		94	2	x	65		1	50	9	2	25	9	5	20	17	9	23	12	4	52	43	15	100	34	16	125	44	19	104	26	9	127	21	6
Taeniorhynchus fasciolata				7			10			2			10	x		17	x		14			45	x	1	63	5	2	50	3	x	13	x	x	3	x	
Taeniorhynchus nigricans	37	5	1	115	1	2	125	x		152	4		217	5	4	260	15	8	274	27	9	390	41	15	405	21	14	314	29	9	355	27	10	229	27	9
Taeniorhynchus sp.				1			2																													
Culex sp.																x	x											1			x					
Total Culicini	115	8	1	217	3	3	203	x	1	220	18	8	301	27	15	319	50	22	357	47	19	494	91	35	573	62	36	408	79	30	475	56	20	359	49	15
Tribe Sabethini																																				
Trichoprosopon sp.																									x					x	2			1		
Wyeomyia (Wyeomyia) sp.							2						12			10	x	x	11	1		15	3	x	9	x		6	1	x	3					
Wyeomyia (Dendromyia) sp.																		x	1			1	x		3	2	x	5			3			x		
Limatus sp.													x																							
Sabethes (Sabethes) sp.											x			x										x												
Sabethes chloropterus															x		x	1	1	1	1	1	x	5	x		2	x	2		x	x	x			
Total Sabethini	0	0	0	0	0	0	2	0	0	0	x	0	13	x	x	10	1	3	13	2	1	17	4	6	13	2	3	12	3	1	8	x	x	2	0	0
Tribe Anophelini	2	0	0	29	x	0	3	0	0	3	0	0	34	0	0	13	0	x	16	0	0	11	1	2	60	2	x	15	1	1	8	0	0	x	0	0
Total All Species	117	8	1	247	4	3	209	x	1	223	19	8	349	28	15	342	51	26	386	49	20	522	96	43	647	65	40	525	83	32	490	56	21	362	49	15

"x" indicates less than 1 mosquito per 10 man hours.

to a common denominator—the number of mosquitoes taken per ten man hours. Fractions of whole numbers were not used in the preparation of these tables, thus the totals of the individual species only approximate the sums recorded under the larger categories listed, such as the tribes. The study was started during the middle of the dry season when the forest mosquito populations were at their lowest ebb and there had been no opportunity for a preliminary reconnaissance of the region during the preceding rainy season, when conditions were more favorable for these insects. The sites of the stations were therefore, selected only with a general knowledge of the region, in an attempt to select sites representing as diverse situations with regard to rainfall, elevation, and geography within the region as would permit weekly access over all weather roads.

Dry Season: The catches during the dry season months of February, March and April were understandably low. Very few *Haemagogus* mosquitoes were taken during these months. *Haemogagus spegazzinii falco* was not taken at all. *Aedes leucocelaenus* was taken only once, at station D, which was our highest station and in an area of higher rainfall than the other Pacific side stations. Such ground pool breeding species as *Aedes taeniorhynchus*, *Psorophora lutzii*, and *Taeniorhynchus titillans* were present in moderate numbers at stations at low elevations. The sabethines were rare, but of the species taken, *Sabethes chloropterus* seemed best able to withstand the dry season conditions.

Rainy Season: With the onset of the rains in May there was an abrupt rise in the populations of *Haemagogus* mosquitoes. At all the stations where collections were made throughout the year, May, June and July, the first three months of the rainy season were the best months for *Haemagogus*. *Haemagogus equinus*, which was the most abundant species taken at these stations, showed a more pronounced peak during these months than either *H. lucifer* or *H. spegazzinii falco*, although these species also were at the height of their abundance during one or another of these months. While it is not evident from the monthly rainfall data, there were periods of several days or more during August when there was no rain interspersed with days of heavy rainfall, and this seems correlated with a general drop in numbers of *Haemagogus* taken during this month. At these stations *Haemagogus equinus* remained at relatively low levels throughout the remainder of the rainy season. *Haemagogus lucifer*, on the other hand, recovered, and demonstrated a second peak of abundance during the last half of the rainy season. From the data in Table IV, recording the catches from the supplementary stations H and J, made only during the last part of the rainy season, it is evident that at this time of year here too *H. lucifer* outnumbers *H. equinus*. *Haemagogus spegazzinii falco*, which is a much less abundant species than the other two, seems to be more uniformly distributed throughout the rainy season, following a slight peak in June and July.

Aedes leucocelaenus demonstrates a somewhat different cycle of abundance than the *Haemagogus* species. It appears with the onset of the rains in May, but rather than immediately rising to a peak as in the case of *Haemagogus*, it rises in numbers more gradually with the greatest number being taken in general in September and October. An exception to this overall picture is the condition at station C where there was a peak in June, but this was exceeded by the subsequent peak at this station in September. Other members of the subgenus *Finlaya* were not present in sufficient numbers to warrant any conclusions about their seasonal incidence.

Aedes serratus which was largely confined to station A became abundant there in June and maintained a high level of abundance during the following two months, with a moderate decline in September to a level at which it persisted for the remainder of the wet season. The occurrence of *Aedes taeniorhynchus* was confined to the first three months of the rainy season, May, June and July, with a tremendous peak at the Pacific side sea-level station A, in June. The other *Aedes* of the subgenus *Ochlerotatus* were not present in sufficient numbers to warrant discussion.

The seasonal cycle of *Psorophora ferox* is best demonstrated at station A (Table V). Here it was abundant throughout the rainy season but with a peak in June, a decline during the period of irregular rains in August, and a second but lesser peak in November. *Psorophora lutzii* was rather evenly distributed in terms of total numbers at all three of the low altitude stations A, E and F. At stations A and E the species was most abundant at the beginning of the rainy season in May and June with very few specimens taken thereafter, while at station F it persisted until November. Probably because of the less severe dry season on the Caribbean coast at station E, ground pools were filled more rapidly with the onset of some rainfall in April, so that this species appeared there in numbers during this month ahead of the rise in the populations at stations A and F.

Taeniorhynchus titillans does not present a consistent picture at the different stations at which it was taken. At stations A and B, it had been abundant during the dry season month of February, with lesser numbers during March. At these stations the species remained at relatively low levels throughout the rainy season. At station F, on the other hand, it was relatively uniformly abundant throughout the rainy season, with a slight dip during the dry season months. *Taeniorhynchus fasciolata* was abundant at only two stations, A and F. At both these stations, it built up gradually to a peak of abundance in October and November, near the end of the rainy season. All specimens of *Taeniorhynchus nigricans* came from station F, and follow the cyclic pattern of *T. fasciolata*. The species was abundant throughout the year, but reached a peak of abundance during the latter part of the rainy season.

The species of *Trichoprosopon* were most abundant during the last half of the wet season. The *Wyeomyia* (*Wyeomyia*) species were taken throughout the rainy season, with a tendency to fall away in numbers toward the end of the year. The numbers of *Wyeomyia* (*Dendromyia*) were, at most stations, too few to be of significance, but the bulk of the catches were toward the end of the wet season in October and November. *Sabethes* (*Sabethes*) species were also too low in numbers to give a clear picture of seasonal fluctuation. They appear to be most prevalent, however, during the last half of the wet season. *Sabethes* (*Sabethoides*) *chloropterus*, which had persisted at a low level through the dry season, rose to considerably higher levels during the rainy season and demonstrated a broad peak during the months of June, July and August.

THE VERTICAL GRADIENT IN DISTRIBUTION

In a paper published in 1944, Bugher, Boshell, Roca and Osorno vividly describe how they noted the sudden abundance of *Haemagogus* mosquitoes in a Colombian forest where wood cutters were felling forest trees, and how this observation led them to observe that *Haemagogus capricornii* (= *H. spegazzinii falco*) is primarily an arboreal species. In the same year, Bates, 1944, demonstrated the ground or tree preference of a number of mosquitoes in the Colombian forest in which he worked.

Bates, 1949, in his discussion of the adult habitat, of mosquitoes, reviews the literature that has accumulated from studies in the tropical forests of both the Old and New Worlds demonstrating the definite vertical stratification of various species, and points out that Garnham, Harper, and Highton, 1946, have gone so far as to propose a special term, "acrodendrophily", to apply to the tendency for certain species to haunt the tree-tops. In order to secure a properly representative sample of the forest mosquitoes it was therefore necessary that at each of the adult catching stations established by us, we make provision for the capture of mosquitoes midway up, and in the tree-tops, as well as at the level of the forest floor. This information on the mosquito fauna of the upper levels of the forest was of particular importance, since, in the present state of our knowledge, it is hypothesized that the main reservoir of the yellow fever virus is in the primate inhabitants of the upper levels of the forest cover; and the mosquito inhabitants of this same environment, the forest canopy, are those most likely to be those involved in the maintenance of the disease in its endemic sylvan form. We have, therefore, gathered the necessary data to compare the vertical stratification of forest mosquitoes in our area with that reported by Bates, 1944, and Causey and Dos Santos, 1949, for the same and closely related species in other endemic centers of sylvan yellow fever in South America.

Bates, 1944, and Causey and Dos Santos, 1949, used only a single tree platform for comparison with their ground catches, whereas at each of our regular catching stations platforms were constructed both midway up the tree and near the tree-top in the forest canopy, thus direct comparison may not be made with our data which are based on captures at two platforms instead of the one used by these other workers. General comparisons, however, will be possible. In Table XI are given the captures, per ten man hours, of the principal species and subgenera encountered in the present study at three levels in the forest. These numbers are based on an average from all six of the stations where collections were routinely made on a weekly basis, throughout the year period of study. In this table are also given the percentages of the mosquitoes taken at each level. These percentages were derived from the totals of the mosquitoes captured at the three levels at each station, adjusted for differences in the number of hours that each was operated during the year.

Haemagogus equinus, it will be seen, was about twice as abundant at each of the elevated platforms, 41.6 per cent and 39.2 per cent, as on the ground, 19.2 per cent. There is very little difference between the captures at the middle platform and the top one. In the case of *H. lucifer*, however, the middle platform catches, 28.5 per cent, were very close to those of the ground-level, 26.0 per cent, while substantially more of these mosquitoes were taken at the top-level platforms, 45.5 per cent. *Haemagogus spegazzinii falco* showed a more marked preference for the higher levels in the forest with a little more than half, 51.0 per cent, of the total catch being made at the top platforms. The middle level platforms in turn captured significantly more, 30.6 per cent, of this species than were taken at ground-level, 18.4 per cent. It would appear then that of the three *Haemagogus*

TABLE XI

Vertical distribution of diurnal mosquitoes

STATIONS	MOSQUITOES PER TEN MAN HOURS			PER CENT		
	Ground	Middle	Top	Ground	Middle	Top
Tribe Culicini						
Haemagogus equinus	4.0	8.7	8.2	19.2	41.6	39.2
Haemagogus lucifer	3.3	3.7	5.9	26.0	28.5	45.5
Haemagogus spegazzinii falco	.6	.9	1.6	18.4	30.6	51.0
Aedes leucocelaenus	1.5	1.2	.9	41.7	33.0	25.3
Aedes leucotaeniatus	.2	.1	x	54.0	35.2	10.8
Aedes terrens	x	x	x	68.0	0.0	32.0
Aedes taeniorhynchus	18.1	.2	x	98.6	1.3	0.1
Aedes serratus	16.1	1.2	.7	89.4	6.4	4.1
Aedes septemstriatus	x	x	x	79.5	10.2	10.2
Psorophora ferox	17.4	4.2	5.8	63.6	15.2	21.2
Psorophora lutzii	2.0	.9	.8	52.9	25.1	22.0
Taeniorhynchus titillans	36.1	4.4	1.8	85.4	10.3	4.3
Taeniorhynchus fasciolata	18.9	3.3	1.3	80.4	14.0	5.6
Taeniorhynchus nigricans	42.9	30.6	12.4	90.9	6.5	2.6
Tribe Sabethini						
Trichoprosopon sp.	2.0	.9	.8	53.9	24.5	21.6
Wyeomyia (Wyeomyia) sp.	4.2	.9	.6	73.8	15.2	11.0
Wyeomyia (Dendromyia) sp.	1.4	.1	.3	74.8	7.6	17.6
Sabethes cyaneus	.3	.5	.5	24.5	40.1	35.3
Sabethes tarsopus	.1	.2	.4	7.5	31.7	60.8
Sabethes chloropterus	1.3	5.8	6.6	9.6	42.4	48.1
Tribe Anophelini						
Anopheles sp.	3.3	.1	.1	94.2	3.3	2.5
Chagasia bathanus	x	x	x	15.0	23.0	62.0

"x" indicates less than 0.1 mosquito taken per 10 man hours.

taken in substantial numbers in the forest *H. spegazzinii falco* shows the greatest preference for the uppermost level.

Aedes leucocelaenus shows a progressive decline in numbers from the ground to tree-top level, but substantial percentages, 33.0 per cent and 25.3 per cent, of the catches are from the tree platform levels. The number *A. leucotaeniatus* taken was so small, 37 for the whole year, that the percentages derived may not be significant, other than to indicate that this close relative of *A. leucocelaenus* shows a similar vertical stratification, with progressively fewer mosquitoes at the higher platforms. Only 25 *A. terrens* were taken throughout the entire year, less than 0.1 per ten man hours at all levels, but of these, twice as many, 68.0 per cent, were from the ground, as from the upper platforms, 32.0 per cent. So few specimens were taken that the failure to capture any at the middle platforms is of no significance. Unlike the foregoing *Aedes* of the subgenus *Finlaya*, the two species of the subgenus *Ochlerotatus* show a very pronounced affinity for the ground-level. *Aedes taeniorhynchus*, with 98.6 per cent of the catch taken on the ground, is the most pronounced ground haunting species encountered. In the case of *A. serratus*, with 79.5 per cent of the catch at ground-level, the stratification is somewhat less pronounced. It should here be noted that the catches of mosquitoes on elevated platforms in the case of such obviously low-level inhabiting species as these, are higher than might be expected under undisturbed conditions in the forest. To reach their platform stations, the field collectors of course climbed up from the ground, and, when such *Aedes* mosquitoes as these were abundant on the ground, it was obvious that some mosquitoes followed the men up to these catching stations to bite there. This fact is reflected in the fact that the upper-level catches of such species as these were recorded in the main during the hour period immediately after the collectors took their stations, in the morning and at midday. This source of error is one which presumably effects in about equal measure the results obtained with regard to all the essentially low-level species.

Psorophora ferox proved also to be an inhabitant of the ground-level with 63.6 per cent of the catch recorded there, while *P. lutzii* showed somewhat less preference for the ground, with about one half, 52.9 per cent, of the catch being taken there, while about a quarter, 25.1 per cent, and 22.0 per cent, was taken at each of the elevated platforms. The somewhat greater tree-haunting habits of *P. lutzii* in comparison with *P. ferox* confirms the similar records of Causey and Dos Santos, 1949, in Brazil, where they found the percentage of *P. lutzii* in trees to be a little more than twice that of *P. ferox*.

The species of *Taeniorhynchus* demonstrated a ground-level preference of about the same order as that shown by the *Ochlerotatus* subgenus of *Aedes*. For each of the three speices, *T. titillans*, *T. fasciolata*, and *T. nigricans*, a decreasing percentage of the total catch was taken at successively higher platforms, but the great bulk of the catch, 80.4 per cent to 90.9 per cent, was taken on the ground.

About one half, 53.9 per cent, of the *Trichoprosopon* appeared in the ground-level catch, about a quarter, 24.5 per cent, in the middle-level catch, and about a fifth, 21.6 per cent, in the high-level catch. These results are very similar to those obtained for *Psorophora lutzii*.

Both subgenera of *Wyeomyia* showed a marked preference for the ground-level with 73.8 per cent, of the subgenus *Wyeomyia* and 74.8 per cent of the subgenus *Dendromyia* being taken there, but they were not so strictly confined to the low-level as *Aedes taeniorhynchus* or *Aedes serratus*.

Our *Sabethes* are of two subgenera, with the subgenus *Sabethes* being represented by the species *cyaneus* and *tarsopus*, and subgenus *Sabethoides* by the one species *chloropterus*. Bates, 1944, found *Sabethes cyaneus* to prefer the ground level, with only 28 per cent of his catch being made in trees. In contrast, we took only 24.5 per cent of the catch of this species on the ground, 40.1 per cent at the middle platform, and 35.3 per cent at the top platform, which would indicate that in our area the species shows a slight preference for the upper-levels. Our results with regard to *S. tarsopus*, indicate that this species shows a strong preference for the upper levels, as we took only 7.5 per cent of the catch at the ground level, and 92.5 per cent of them at the two elevated platforms. *Sabethes chloropterus* of the second subgenus, *Sabethoides*, shows a marked preference for the upper levels, with only 9.6 per cent of the catch from the ground. This confirms Bates, 1944, results with the closely related *S.* (*Sabethoides*) *imperfectus*. It is noteworthy that we found both *S. tarsopus* and *S. chloropterus* to show an even more marked stratification in favor of the higher-levels than *H. spegazzinii falco*, as did Bates, 1944. It is also of interest that in the case of this genus, the habits of the species, with regard to vertical stratification, breaks across subgeneric lines. *Sabethes cyaneus* and *S. tarsopus*, are indeed closely related species, yet the former appears relatively uniformly distributed at all levels, while the latter shows preference for the upper levels. This is a point also previously noted by Bates, 1944.

The *Anopheles* taken were so few in number that we have combined them all in Table XI. It will be seen that they are quite strictly limited to the forest floor with 94.2 per cent being taken there. Only *Aedes taeniorhynchus* showed a greater preference for the ground-level. In striking contrast, is the other anopheline genus, *Chagasa*, which showed a marked preference for the upper-levels with 15 per cent of the catch being from the ground and 85 per cent from the two tree platforms. This is, in general, a confirmation of the results reported by Causey and Dos Santos, 1949, who found only 2.2 per cent of their *Anopheles* on tree platforms and 17.0 per cent of *Chagasia* at the upper levels.

In Table XII these species and subgenera are arranged for ready reference in descending order with regard to the proportion captured, at ground levels. They are also broken into five rather arbitrary categories, which will, however prove useful in discussions of these species in relation to their possible involvement in the cycle of sylvan yellow fever.

A point of which we have not presented data here, which was considered of significance in the epidemiology of sylvan yellow fever, by South American workers, is the possible shift in altitudinal preference of the arboreal species to the ground level during dry season, as the microclimate of the forest canopy, characterized by high light levels and temperatures, and low humidities, are more closely approximated on the forest floor at that time of year. Such a shift has been reported by Bates, 1944, working in a high rainfall forest only 4 degrees from the equator, but was not found to be the case in the area in Brazil worked by Causey and Dos Santos, 1949, which is 20 degrees south of the equator and on an interior plateau 700 meters in altitude. In the latter case the dry season coincided with cool weather which Causey and Dos Santos considered to have modified their results. In our area the dry season, covering the four months of

January through April, is so extreme that few or no tree hole breeding mosquitoes, which are the inhabitants of the upper forest levels, are present as adults. The numbers of arboreal mosquitoes were too few during the dry season to afford sufficient material for a profitable comparison with the wet season catches.

TABLE XII

Diurnal Mosquitoes Arranged With Regard to Their Vertical Distribution in a Tropical Forest

(Per cent of catches made at ground-level are indicated before each species)

Predominantly ground-level with insignificant arboreal catches;		
	98.6	*Aedes taeniorhynchus*
	94.2	*Anopheles* sp.
	90.9	*Taeniorhynchus nigricans*
	89.4	*Aedes serratus*
	85.4	*Taeniorhynchus titillans*
	80.4	*Taeniorhynchus fasciolata*
	79.5	*Aedes septemstriatus*
Predominantly ground-level but with substantial arboreal catches;		
	74.8	*Wyeomyia* (*Dendromyia*) sp.
	73.8	*Wyeomyia* (*Wyeomyia*) sp.
	68.0	*Aedes terrens*
	63.6	*Psorophora ferox*
	54.0	*Aedes leucotaeniatus*
	53.9	*Trichoprosopon* sp.
	52.9	*Psorophora lutzii*
Relatively indiscriminate but favoring the ground-level;		
	41.7	*Aedes leucocelaenus*
Relatively indiscriminate but favoring the arboreal situation;		
	26.0	*Haemagogus lucifer*
	24.5	*Sabethes cyaneus*
Predominantly arboreal;		
	19.2	*Haemagogus equinus*
	18.4	*Haemagogus spegazzinii falco*
	15.0	*Chagasia bathanus*
	9.6	*Sabethes chloropterus*
	7.5	*Sabethes tarsopus*

RELATION TO YELLOW FEVER IN THE AREA

Information involving mosquitoes as vectors of yellow fever is of several sorts, from such insubstantial evidence as their ability to retain virus but failure to transmit it by bite, to the capture of mosquitoes in nature which do prove able to transmit the virus by bite. Full bibliographies of the several lines of investigation on the potential vectors of sylvan yellow fever in South America are given in Laemmert, Ferreira and Taylor, 1946, and Bates, 1949, and will not be repeated here. We will list, however, those species taken in the present study, on which incriminating evidence of one sort or another is available.

The following species have been infected in the laboratory, but failed to transmit the virus by bite: *Aedes terrens*, *A. serratus*, *Taeniorhynchus titillans*, *T.*

fasciolata, and *Psorophora cingulata*. The following have been infected in the laboratory and transmitted the virus by bite: *Haemagogus equinus*, *H. spegazzinii falco*, *Aedes leucocelaenus*, *A. fluviatilis*, *A. taeniorhynchus*, and *Psorophora ferox*. The following have been found infected in nature and transmitted the virus by bite: *Aedes leucocelaenus*, *Haemagogus spegazzinii falco*, and possibly *H. equinus* and/or *H. lucifer*. The evidence with regard to *H. equinus* and *H. lucifer* in this last connection is uncertain, as these two species were a portion of a group including *H. spegazzinii falco* as well, which immunized a rhesus monkey following biting (Boshell and Osorno, 1944). In addition, virus has been recovered by inoculation from a mixed group of 88 sabethine mosquitoes including *Sabethes* (*Sabethoides*), *Limatus*, *Wyeomyia*, and *Trichoprosopon* (Shannon, Whitman and Franca, 1938).

Recently, Waddell, 1949, has reported experiments in which the *relative* ability of certain of these mosquitoes to transmit yellow fever virus was tested. Assuming a transmission rate of 1.00 for *Aedes aegypti*, the classical vector of the disease, she obtained transmission ratios for other species which also occur in our area as follows: *Aedes leucocelaenus*, 1.29; a mixed group of *Haemagogus capricornii* and *H. spegazzinii*, 0.73; *H. equinus*, 0.45; and *H. splendens*, which is closely related to our *H. lucifer*, 0.16.

Thus we see that the evidence from the field coincides with the data on the relative efficiency of the species as vectors in the laboratory, *Aedes leucocelaenus* and *Haemagogus spegazzinii*, both of which have been found infected in nature and transmitted the virus by bite, are also the most efficient vectors of the virus in the laboratory, while *H. equinus* and *H. splendens* are less efficient vectors in the laboratory, and remain unproven in the field as vectors. We have no direct evidence on which of the mosquitoes taken in our study may be the vector or vectors in this area, but, keeping in mind the information summarized above, we may profitably examine these species in the light of the data we have gathered on them.

Haemagogus equinus and *H. lucifer* were not only the most abundant representatives of this genus in the area, but also the greatest numbers of them were taken at stations nearest the fatal human cases of yellow fever. Both are, of course, sufficiently arboreal to satisfy the theoretical requirements of a sylvan yellow fever vector on that score. On the other hand, the peak of their abundance was in the first part of the rainy season when cases of yellow fever were not recorded, although *H. lucifer* did demonstrate a second lesser peak later in the rainy season when the human cases did occur. In terms of absolute numbers, *H. lucifer* was at higher levels of abundance during the months of August, September, November, and December, when all but one of the yellow fever fatalities occurred, than *H. spegazzinii falco*, the proved South American vector. During these months *H. equinus* also exceeded in numbers *H. spegazzinii falco* at station B near the edge of the forest, but *H. spegazzinii falco* about equalled, or exceeded *H. equinus* at station C deep in the forest. *Haemagogus spegazzinii falco*, while low in numbers in comparison with the other two *Haemagogus* which occurred in the forest, was present, nevertheless, throughout the rainy season at a rather uniform level, following a small peak after the beginning of the rains. A point which would perhaps lend credulence to the hypothesis that this species is a vector in this area is the fact that the actual number of yellow fever cases has been so small. It is of interest at this point to compare the maximum monthly capture rates of these *Haemagogus* mosquitoes with those obtained in other endemic centers of sylvan yellow fever in South America. Causey and Dos Santos, 1949, working in Brazil, record a maximum monthly rate per man hour of 5.0 for *H. spegazzinii*, while Laemmert, Ferreira and Taylor, 1946, also in Brazil, report a maximum rate of 7.96 per man hour for a *Haemagogus* population thought to be predominantly, if not entirely, *H. spegazzinii*. Bates, 1944, on the other hand, has recorded very much higher rates from his study area in Colombia, where he took as many as 140 per man hour of *H. capricornii* (= *H. spegazzinii falco*) on a particularly favorable day, and an average of 43.4 per man hour during a favorable three-month period. Our data indicate rates closer to those found in Brazil than those reported from Colombia. The maximum monthly rate we found for *H. equinus* was 5.3 per man hour at station C-44 in June, 1949; for *H. lucifer*, 5.2 per man hour at station H-1 in October, 1949; and for *H. spegazzinii falco*, 1.6 per man hour at station B-46 in July, 1949. While the data given in Table IX for station E would indicate higher rates, it must be remembered that this station was operated only from 10:00 A.M. to 12:30 P.M., a most favorable time of day for the activity of *Haemagogus* mosquitoes, and these data may not, therefore, justifiably be compared with those from other stations operated throughout the day, including, within the average, catches from a number of less favorable hours. From these comparisons it is evident that the maximum densities of *H. equinus* and *H. lucifer* in our area are similar to ones reported from other endemic centers of sylvan yellow fever in Brazil, but lower than the densities reported from Colombia. *Haemagogus spegazzinii falco*, on the other hand, was present only at much lower densities. It must be noted, however, that what we record here are not truly "densities" of the populations of these mosquitoes, but only the relative numbers attacking man. It may be that these mosquitoes may have preferred hosts for blood meals about which we have no information. Yet, as we are interested in evaluating the possible role of these insects as vectors of a human disease, for our purposes, these data involving man as the bait are probably valid.

It is well to keep this point in mind, however, in evaluating the ability of these mosquitoes to carry the virus through the unfavorable dry season. We have concluded above that it is difficult to conceive that these mosquitoes could maintain the virus then, since they seem to all but disappear during the dry season. We cannot exclude the possibility that they may have other preferred hosts during the dry season, about which we know nothing.

Haemagogus chalcospilans and *H. argyromeris*, as we have shown elsewhere in this paper, are also common mosquitoes in this area, but they may be excluded from our consideration as possible vectors of sylvan yellow fever since they do not invade the forest to bite man.

Aedes leucocelaenus appears to be only about as abundant as *H. spegazzinii* *falco* and in certain regards seems to fit the requirements for the vector from animal host of the virus to man better than *H. spegazzinii falco*. First is the fact that the species is relatively indiscriminate with regard to vertical stratification, for 41.7 per cent were taken on the ground while 33.0 per cent were from the middle platforms and 25.3 per cent from the top platforms. The human yellow fever fatalities were individuals working in and at the edge of the forest, but they were not wood cutters. This would seem to favor as a vector a mosquito like *A. leucocelaenus*, which become infected by feeding on monkeys in the forest canopy and subsequently bite man at ground-level, even though the man was not disturbing the forest canopy by chopping down trees. *Haemagogus spegazzinii falco*, on the other hand, was predominantly an upper-level mosquito with only 18.4 per cent of the catch being taken at ground-level, 30.6 per cent at the middle platforms and 51.0 per cent at the top platforms. Second is the fact that according to the work of Waddell, 1949, *A. leucocelaenus* is even more efficient as a vector of yellow fever virus than *A. aegypti*. Third is the circumstance that this species rose to its peak of abundance in the latter part of the rainy season which is the time when the yellow fever cases occurred. The point which remains open to doubt is whether this species is at any time present in sufficient numbers to maintain the virus. Other *Finlaya* mosquitoes such as *A. terrens* and *A. fluviatilis* are too rare to warrant consideration. Of the aedine subgenus *Ochlerotatus*, both the species *A. serratus* and *A. taeniorhynchus* are abundant, but they may be discounted for two reasons. First, they are most abundant at the sea-level station A, where the disease did not occur; and second, they are predominantly ground-level species with insignificant arboreal representation.

Psorophora cingulata may be eliminated from consideration because it is rare, and *P. ferox*, because it was abundant where the disease did not occur and uncommon at the stations near the human fatalities. *Taeniorhynchus titillans* was abundant at station B, near one of the cases, but it is predominantly a ground-level species with insignificant arboreal catches. *Taeniorhynchus fasciolata*, while abundant at the near sea-level stations A and F, was rare at the stations near where the disease occurred, and in addition is predominantly a ground level inhabitant. Of the Sabethines, it is interesting to speculate about the species of the genus *Sabethes*, particularly *S. (Sabethoides) chloropterus*. This species was present in substantial numbers, there being about four times as many specimens taken at the stations operated throughout the year as either *H. spegazzinii falco* or *A. leucocelaneus*. It was most abundant at station B, near the location of one yellow fever death, and also present in substantial numbers at the H stations near the location of other human fatalities. In addition, it persisted through the dry season months when *Haemagogus* and *Aedes leucocelaenus* were rare or wholly absent, and it is a species which is predominantly arboreal. It is unfortunate that there are available no published laboratory results of experiments to determine its ability to transmit yellow fever virus, although it is known that a *Sabethoides* was one of the species in a pool of sabethine mosquitoes taken in nature, which was proved to be carrying virus (Shannon, Whitman and Franca, 1938). In light of its habits and distribution in relation to the epidemiology of yellow fever in our area, it should be considered a suspect until evidence otherwise is forthcoming. The other two *Sabethes* in our area appear not to be sufficiently abundant to be likely prospects as vectors of the disease to man.

SUMMARY

There are recorded here the distribution, the annual cycle of abundance, the vertical stratification in the forest, and the possible relationship of the forest mosquitoes attacking man to the transmission of sylvan yellow fever following an outbreak of this disease in Panama. Particular attention is directed toward species of mosquitoes which are proven vectors of sylvan yellow fever in South America, *Haemagogus spegazzinii falco* and *Aedes leucocelaenus*.

Haemagogus equinus and *H. lucifer* proved to be considerably more abundant than *H. spegazzinii falco* or *Aedes leucocelaenus*, but, because of the small number of cases of yellow fever despite the considerate number of nonimmune persons exposed in the recent outbreak, it is suggested that these two last mentioned species may be the ones involved in the transmission of the disease to man in this area. As all of these species virtually disappear as adults during the dry season the question remains open as to how the virus is maintained during this unfavorable time of year. Two other species of *Haemagogus* taken in the study area, *H. chalcospilans* and *H. argyromeris*, were present in some abundance in the open or light second growth situations, but did not invade the forest to bite, and seem to be disqualified as vectors by the nature of their habits. The only other species which the evidence seems to render suspect is *Sabethes chloropterus*. This species demonstrates in its habits many of the characteristics of *Haemagogus*, is present in significant numbers, and seems better able to carry through the unfavorable dry season. There is, however, no direct evidence as to the ability of this species to transmit the yellow fever virus.

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